What's an internal clock for? From temporal information processing to temporal processing of information

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Abstract

The existence of an internal clock and its involvement in information processing has been investigated in humans using the experimental protocol of Treisman et al. (1990) [Treisman et al., 1990. Perception, 19, 705 – 743]. In this protocol, a periodical stimulation, which is assumed to drive an internal clock, is delivered during a reaction time (RT) task. The accelerating or slowing down effects of the periodical stimulation, according to its frequency, allowed an estimate to be made of a simple harmonic of the frequency of the internal clock. The estimate was close to 21 Hz. In the framework of the serial model of information processing, the present work investigates the involvement of the internal clock in the transmission of information between processing stages during RT. The data tend to support the idea that the internal clock allows the transfer of information from one stage to the next one at definite moments only, periodically distributed in time. According to our results, and recent data from the literature on electric cortical oscillations, we propose a model of an internal clock sending periodic inhibition, which would permit an increased signal/noise ratio in the processing and the transmission of information in the central nervous system.

Keywords: Human; Internal clock; Cortical oscillations; Reaction time; Transmission of information

1. Introduction

The way we estimate time with accuracy is still a matter of debate, and the question of the existence of a mechanism devoted to this purpose (i.e. an internal clock) is still open. Nevertheless, the idea that an internal clock does exist has become increasingly popular during the last few years, and several models have been proposed. Among these models, a particular class is based on the idea that a pacemaker sends periodic impulses to an accumulator (Church, 1984). The perceived time is a function of the number of impulses stored in the accumulator. If theoretically possible, as Treisman et al. (1990) said, this kind of model would be "strengthened if we could present a model for the pacemaker from which testable predictions could be derived, and if we could estimate the basic theoretical parameter of such a model, the frequency of the pacemaker" (Treisman et al., 1990, pp. 705–706). Treisman's model is composed of two parts: a temporal oscillator and a calibration unit. The temporal oscillator, modeled as a set of three interactive neurons, sends periodic pulses, at a stable frequency Fo, to the calibration unit. The calibration unit multiplies Fo by a calibration coefficient Cf. The pacemaker output is the adjusted frequency $Fp = Cf \times Fo$. This yields a stable, but easily adjustable frequency. Treisman and collaborators hypothesized that even if the temporal oscillator should be protected from outside influences to keep its frequency stable, a strong enough periodic stimulation should influence it if the frequencies are close. In this case a phase setting will occur, which will slow down the internal frequency if the external stimulation is lower than Fo, and speed it up in the opposite case. If the external frequency varies step by step, we should observe successively: (1) no driving effect on the internal clock when the external frequency is far below the internal one; (2) a slowing down of the internal clock when the external frequency is just below Fo; (3) no effect when the external stimulation is Fo (or an harmonic); (4) an increase in the internal frequency when the external one is higher than Fo, and (5) no effect when the external frequency is far higher than Fo. Fig. 1a shows such a pattern of clock frequency variations.

This model has been tested in a duration estimation and production tasks (Treisman et al., 1990; Treisman and Brogan, 1992). These authors obtained systematic modulations of the timing performance according to the external stimulation frequency. Further, in a reaction time (RT) experiment, Treisman et al. (1992) obtained a more striking effect: the performance was modulated by the frequency of the external stimulation, that is, for some frequencies the RT was increased, and for the immediate following frequencies, it was decreased. Thus the performance presented some interference patterns (see Fig. 1a). This result suggests that the putative internal clock would influence the information processing system taken as a whole. A

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*Abbreviations: C, correct electromyographic activity latency; CS, correct – success trials; CT, correction time; EMG, electromyography; FP, foreperiod; I, incorrect electromyographic activity latency; ICS, incorrect – correct – success trials; LED, light emitting diode;MT, motor time; RS, response signal; RT, reaction time.

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fascinating point of these behavioral studies is that estimations of the internal clock frequency (Kristofferson, 1984; Treisman et al. 1990, 1992, 1994; Burle and Bonnet, 1997) strongly overlap the frequency band of various cortical oscillations recorded concomitant to cognitive activities (Llinás and Ribary, 1993; Pfurtscheller et al., 1993; Titinen et al., 1993). Indeed during the last 10 years, the interest in the study of cortical oscillations has greatly increased with the (re)discovery of fast rhythms (30–50 Hz, i.e. g-band, often called '40 Hz') contingent to cognitive activities. These rhythms seem to exist at several processing levels, from sensory inputs (Gray and Singer, 1989; Titinen et al., 1993; Chrobak and Buzsáki, 1998) to motor outputs (Nashmi et al., 1994; MacKay and Mendonça, 1995). If their involvement in cognitive activities is quite consensual (see nevertheless, Ghose and Freeman, 1992), their precise function still remains unclear. A great number of interpretations have been proposed: temporal binding of the percept (Gray and Singer, 1989); attentional role (Bouyer et al., 1981; Roelfsema et al., 1997); motor preparation (Nashmi et al., 1994). Crick and Koch (1990) have proposed that such oscillations may be the key to consciousness. Some studies have provided evidence that cortical oscillations are due to inhibitory interneurones (Llinás et al., 1991), acting as an internal clock for the pyramidal neurons by permitting them to fire only at defined moments in time (Whittington et al., 1995; Jefferys et al., 1996). These data parallel, at the behavioral level, the analysis of RT distributions which evidenced some periodicities in these distributions (Harter and White, 1968; Dehaene, 1993). Indeed, these data suggest that in a RT task, the responses are more likely to occur at some given moments equally spaced in time, and thus that an oscillatory mechanism gates the response of the subject, permitting the response only in some phase of the oscillation.

Thus, if we accept that the internal clock hypothesized by cognitive psychologists has something to do with these fast oscillations, then this internal clock should not only be used to estimate time, but should have a more general role, and this could account for the results obtained by Treisman et al. (1992) in the RT experiment. Furthermore, this could led to an alternative ex-

planation for the effect of divided attention on temporal processing (Zakay, 1992; Casini and Macar, 1997): Indeed, it is generally assumed that the judgement of time depends on the accumulation of impulses in an accumulator. In this popular view the impulses are only used for temporal processing and divided attention effects are due to the lost of some impulses during the processing of the second task. Now, if impulses are not only used for temporal tasks, but also for non-temporal tasks, then, in dual task situations, some impulses of the clock should be used by the non-temporal task, thus leading to a reduction of the number of impulses stored in the accumulator (see Casini and Macar, 1999, this issue). In addition, the data obtained by Treisman et al. (1992) on RT points to interesting questions on the role of a timing mechanism in the informa- tion processing system. The RT is classically decomposed in stages (or level)1 of processing. Theios (1975) proposed a decomposition in five stages: stimulus detection, identification, stimulus – response association, response programmation, and execution. In the discrete conception of information processing (Sternberg, 1969; Sanders, 1990; Roberts and Sternberg, 1992), there is no temporal overlap between these various stages, and hence, the RT is the arithmetic sum of the durations of the various stages. In this case an increase in RT is due to an increase in the duration of one or more stage(s). In a previous study (Burle and Bonnet, 1997), we investigated the stages which are influenced by the internal clock. For this purpose, we used the additive factors method (Sternberg, 1969). The rationale of this method is that if two factors affect two different stages, then the combination of these two factors should lead to an effect which is the sum of the two separate effects. On the contrary, if they affect at least one stage in common, their combination should lead to an effect higher than the sum of the two separated effects. Thus, if the internal clock affects one stage, the duration of this stage should vary according to the external stimulation frequency supposed to drive the clock, and this effect should interact with some other factors known to affect this stage. For this purpose, 11 click train frequencies, from 19.4 to 25.4 Hz with a 0.6-Hz step, were used to drive the internal clock. They were presented before and during the RT. Three factors known to affect sensory (signal intensity), decisional (stimulus – response spatial compatibility) and motoric (response repertoire) stages were used. We obtained the predicted pattern (similar to the one schematized in Fig. 1a) of performance variations for three positions of the frequency band: between 20.6 and 21.2 Hz, between 23 and 23.6 Hz, and between 24.8 and 25.4 Hz. All the subjects presented the interference pattern between 20.6 and 21.2, whereas the two other patterns were more noisy, suggesting that the pattern between 20.6 and 21.2 reflects a more simple harmonic (possiby 0.5, see discussion) of the internal clock frequency than the two others. Nevertheless, no conclusion could be drawn on the stages being influenced, partly because the expected interaction effect (estimated a posteriori) was never above 2 ms. It is thus possible that so tiny an effect could not be evidenced. Another possible reason was that the internal clock could act elsewhere. It could pace the transmission of information from one stage to the next one. If the transmission is discrete (Sternberg, 1969; Sanders, 1990; Roberts and Sternberg, 1992), that is the output representation of a stage is transmitted at once to the subsequent stage, then the quantity of transmitted information will be substantial, and thus a great number of neurons should be involved (Miller, 1988). Synchronous transmissions could be efficiently paced by an internal clock.

The present work was aimed at testing the hypothesis that the internal clock paces the transmission of information from one stage to the next one. In that case, the output of each stage should go through a gate system, and this system should open in a discrete way at given moments periodically distributed in time (Fig. 2). By comparing two categories of trials which differ by the number of processing stages involved, and, hence, by the number of transmissions, we could study the influence on RT of a systematic change in the internal clock's rhythm. According to the standard discrete model, it seems, at first sight, impossible to experimentally manipulate the number of stages. Nevertheless, in studies using bimanual responses and combining behavioral and surface EMG chronometric clues, in some

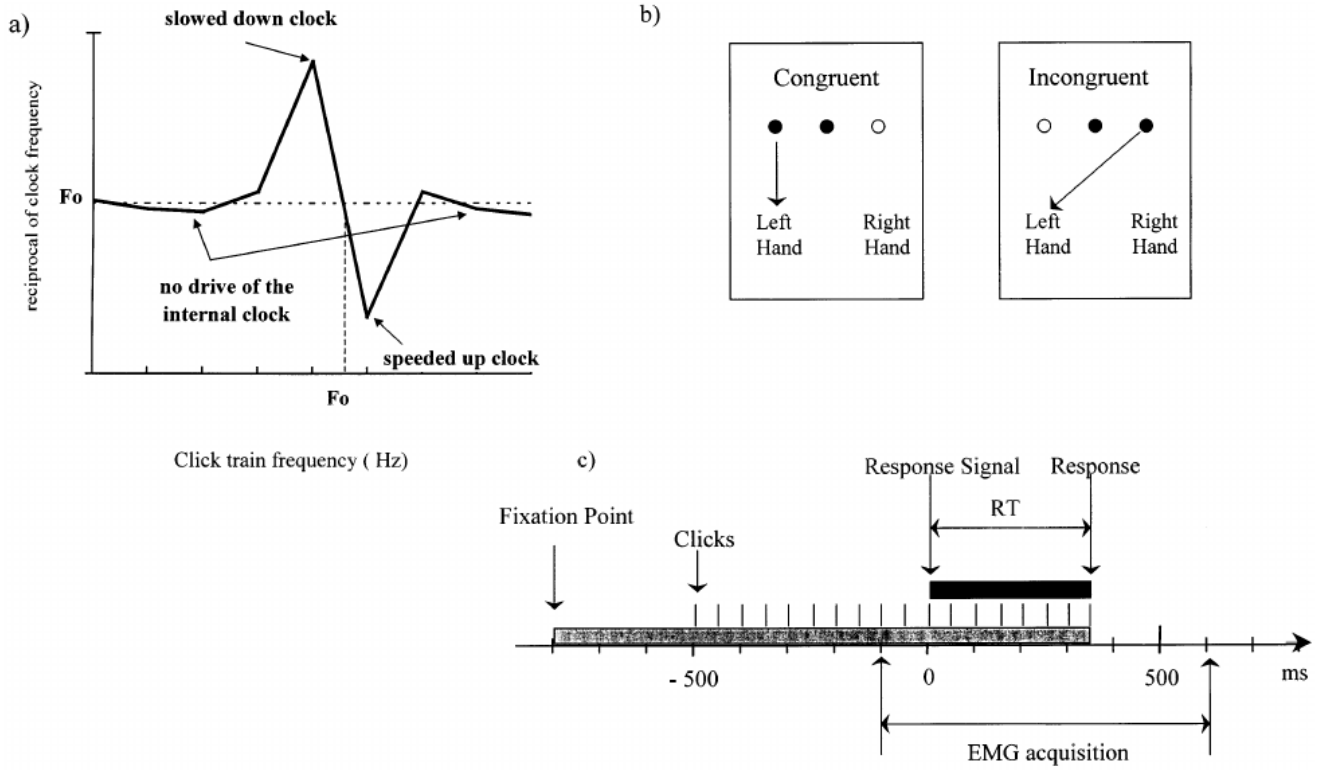

Figure 1: (a) Hypothetical schema of the internal frequency variations (ordinate) driven by an external click train frequency (abcissa).The internal rhythm, with a given frequency Fo, will be entrained by the external stimulation provided that the two frequencies are close. If the stimulation frequency is lower than the internal one, the effect is a slowing down of the internal rhythm, and hence an increase in the processing time. A speeding up will occur if the stimulation frequency is just above Fo. (b) Diagram of the simulus presentation display. The trials could be either congruent or incongruent depending on the spatial correspondence between the position of the RS and the position of the response to be performed, which is colour dependent. (c) Time course of a trial.

trials, EMG activation has been observed on both the correct and incorrect sides (Eriksen et al., 1985). In the majority of these trials, the incorrect activity occurs first. This point was further studied by Smid et al. (1990) in a protocol where the subjects have to respond right or left depending on a target letter (S or H) presented at the center of a display with five letters (Eriksen and Eriksen, 1974). The four surrounding letters could be either congruent with the target (SSSSS or HHHHH) or incongruent (SSHSS or HHSHH). The RT is known to be longer in the last condition because of the conflict between the target and the distractors.2 An interesting result in Smid et al.'s study, even if they do not comment on it, is that, in trials with an incorrect EMG activity, the time elapsing between incorrect and correct activity was longer when the target letter was incongruent with the noise letters than when it was congruent. This suggests that the stage(s) lengthened by the incongruence is reiterated after the occurrence of an incorrect activity, that is, the subject goes back through some processing stages. In those particular trials the number of transmissions should then be increased. It then becomes possible to compare the effects of the driving of the internal clock between trials composed of N stages, and trials composed of $N + X$ stages. The following predictions regarding RT variations can be drawn according to the hypothesis of an increased number of processing stages on the interference pattern of the performance (Fig. 1a). For an illustrative purpose, we will call the delay between two openings of the gate α. As the end of the processing stages is independent, at first sight, from the gate opening, the average transmission time is $\beta = \alpha/2$. In the case of N transmissions, the total average transmission time is

$$N \times \beta \tag{1}$$

If the clock paces the opening of the gate between stages, then a slowing down of the clock increases the delay between two openings by m, causing an increase in the average transmission time (the peak of the interference pattern, Fig. 1a)

$$N(\beta + \epsilon) = N \times \beta + N \times \epsilon \tag{2}$$

In the case of a speeding up of the clock, the opposite effect is expected. The value $(N \times \epsilon)$ reflects the increase in RT due to the slowing down of the clock. The variations of $\pm\ (N \times \epsilon)$ of the RT, determine the amplitude of the interference pattern previously described. Now, if the number of transmissions is increased in some trials, let say $N + X$, the slowing down due to the clock will be

$$(N + X)(\beta \pm \epsilon) = (N \times \beta) \pm (N \times \epsilon) + (X \times \beta) \pm (X \times \epsilon) \tag{3}$$

In this case $(X + \beta)$ is due to the increase in the number of transmission (reflected in the RT), the value $(N \times \epsilon)$ is due to the

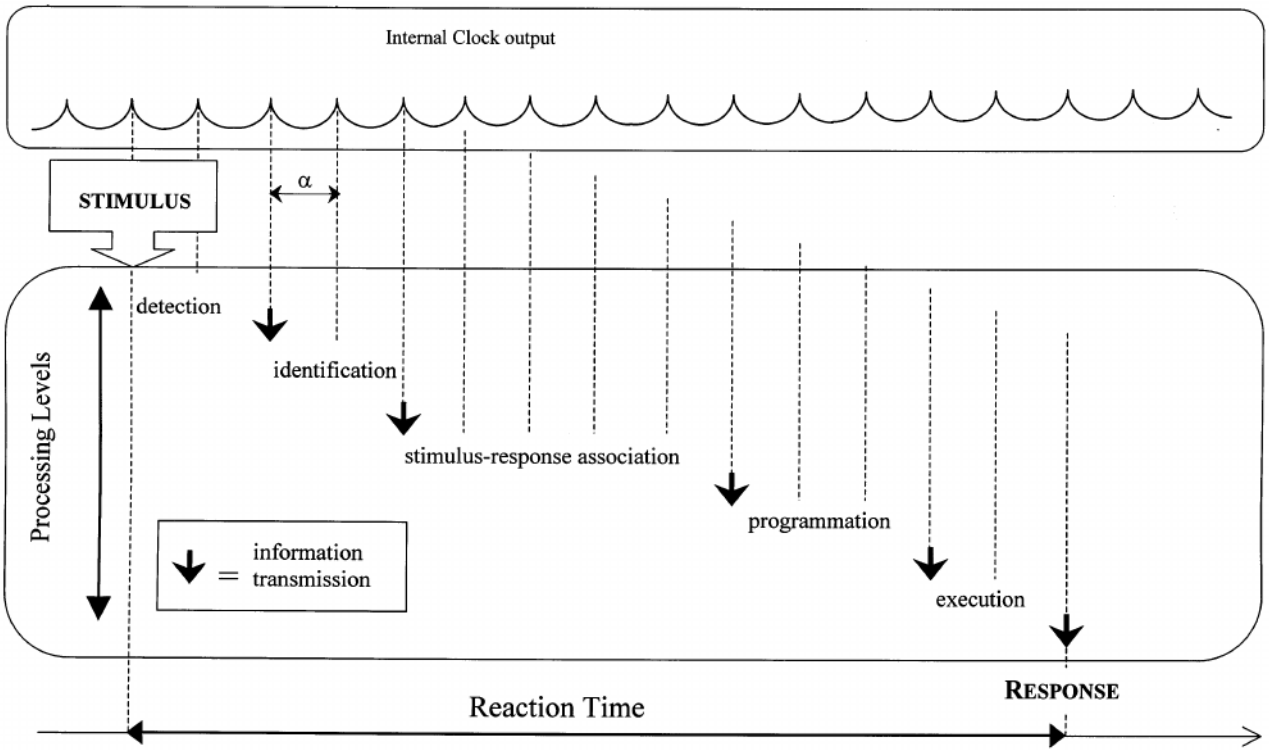

Figure 2: Schema of the hypothetical gating of the between stages transmission by the internal clock in the serial information processing model. The internal clock sends periodic impulses to the information processing system. h: internal clock period. The duration of each operation (detection, identification,...) is symbolically represented by the word length. However, the time of transmission is delayed until the next impulse of the internal clock. The dashed lines represent the possible moments for the transmission to occur, and the solid arrows the actual transmissions.

driving of the clock, which was already present in (2), and $(X \times \epsilon)$ is the interactive term reflected on the amplitude of the interference pattern, which will have as a value $\pm(N \times \epsilon) + (X \times \epsilon)$. Thus, if an internal clock paces the transmissions, an increase in the pattern amplitude should be obtained for trials presenting an incorrect EMG activity. In summary, Burle and Bonnet (1997) evaluated the implication of the internal clock within the various processing stages using the additive factors method. A possible explanation of their results was that the clock paces the transmissions of information from one stage to the next. This hypothesis had been tested in the present experiment.

2. Materials and methods

2.1. Subjects and procedure

Eight subjects, four male and four female, aged from 22 to 29 years (mean: 26 ± 2 years), participated in the experiment. Six subjects were right handed, and two were left handed. They signed informed consents and were paid for participating. In this experiment, we used a 'Simon' task (Simon and Small, 1969), where subjects had to respond with their right or left thumb according to the color (red or green) of the stimulus which could appear on the left or on the right of a fixation point. Therefore, when one of the imperative signals was presented, the trial was either congruent or incongruent depending on whether the correct response was on the same side as the signal or on the opposite side (Fig. 1b). The subject was comfortably seated, 2 m away from three horizontal light emitting diodes (LEDs) 1 cm apart, placed at eye level. The blue central LED was used as a fixation point, and the two lateral ones, which could light on either red or green, were used as response signals. The whole display was contained in a 1.7° vision angle. The responses consisted of thumb presses on force sensors (Interlink Electronics force sensitive resistors; 24 mm in diameter) glued on plastic cylinders (3 cm diameter, 7.5 cm height) which served as hand-grips. The cylinders were fixed 20 cm apart in front of the subjects. The force threshold for responses to be recorded was set at 20 N. Half the subjects (two women, two men) had to respond left when the red LED illuminated and right when the green LED lighted on, the other half had to respond right for red, and left for green. When a response signal appeared, the subject had to press on the force sensor corresponding to the color. The instruction was to respond as fast as possible without making errors. The external periodic stimulations used to drive the clock were 0.1 ms auditory clicks. The subjects were told to ignore the clicks. In a previous experiment (Burle and Bonnet, 1997), the most distinct pattern was obtained between 20.6 and 21.2 Hz. For this reason, we decided to examine more precisely the vicinity of these two frequencies. Six frequencies were chosen, ranging from 19.5 to 22 Hz with 0.5 Hz steps. The order of the frequencies within each block was randomly distributed. The intensity of the click train, recorded at head level, was 75 dB (A). First, subjects un-

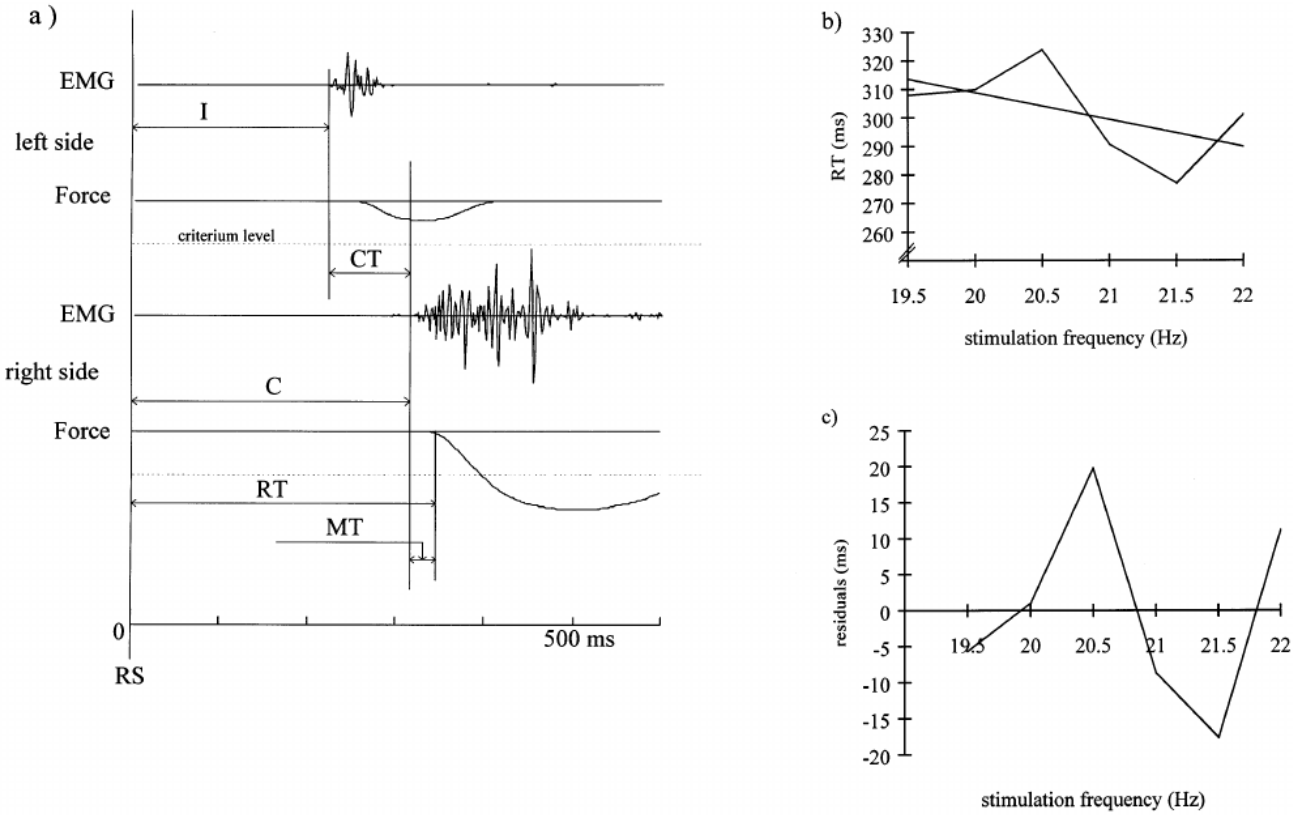

Figure 3: (a) Representative right-hand ICS (incorrect–correct– success) trial with EMG and force recordings for left side (top) and right side (bottom). The left-hand force deviation does not reach the criterion level. Five chronometric indices are defined: (1) RT (reaction time) from the response signal (RS) to the earliest force deviation on the correct right side; (2) C (correct activity latency) from the RS to the EMG onset on the Correct side; (3) MT (motor time) from the EMG onset to the earliest force deviation on the correct side; (4) I (Incorrect activity latency) from the RS to the EMG onset on the incorrect side; (5) CT (correction Time) from the incorrect EMG activity to the correct EMG activity. (b) Raw mean RT as a function of stimulation frequency, and regression slope computed on these data (here on correct activities of ICS trials for one subject). (c) Residual RT after detrending for the same data.

derwent a practice session of four blocks of 56 trials without clicks: 14 repetitions of four conditions (two colors × two positions). They next underwent two experimental sessions. The experimental blocks consisted of 480 trials: 20 repetitions of 24 conditions (two colors × two positions × six frequencies). Trials with incorrect overt response were randomly presented again in the remaining trials. For each trial, the fixation point was illuminated 800 ms before the response signal (RS) (Fig. 1c). Clicks were presented about 500 ms before the RS. To prevent the RS onset between two clicks from affecting the frequency of the sensory stimulation, RS was always synchronized with a click. The time between the beginning of the click train and the response signal was, therefore, frequency-dependent. As a consequence, the time between click train onset and the RS varied between 488 and 524 ms (Section 3). Reaching the force threshold (20 N) on one of the two force sensors stopped the click train and turned the LEDs off.

2.2. *EMG acquisition*

The acquisition of EMG began 100 ms before the RS and ended 600 ms after it (Fig. 1c). Two self-adhesive electrodes Ag-AgCl were placed 2.5 cm apart over the flexor pollicis brevis of both hands. The band width of acquisition was between 70 Hz and 1 kHz, with a sampling rate at 2 kHz. The impedance were always kept below 50 kΩ (at 30 Hz). RT was decomposed into two periods: a first period from RS to the start of the correct EMG activity (C), and a second one, from the beginning of this EMG activity to the onset of the force record, called motor time (MT). In trials with an incorrect EMG activity (Fig. 3a), the time between RS and the onset of incorrect EMG activity was labeled I, and the difference between C and I was called correction time (CT).

2.3. *Classification of trials*

Onsets of both EMG activity and force deflection were detected using the Smid et al. (1990) algorithm. Nevertheless, the algorithm sometimes failed to correctly detect EMG onset. Therefore all the trials were checked and the cursors were sometimes manually set at the visible EMG onset. Of course, the nature of the trial was unknown. It must be noted that the force deflection onset (determining RT) was never modified. Only trials leading to the appropriate response, that is, reaching the force threshold on the correct side first, have been analyzed. They have been called ‘success trials’. Within these ‘success trials’, we separated trials with no incorrect EMG activity (correct – success, CS) and trials with incorrect EMG activity on

the contralateral side at least 10 ms before correct activity (incorrect –correct–success, ICS) (Fig. 3a). These two categories represented 92.3% of the trials. Due to low numbers, trials with incorrect activity after correct activity, and trials with weak activity on the correct side followed by stronger activity giving the appropriate response have been neglected.

2.4. Search for interference patterns

According to Treisman's model, the clicks are supposed to have a non-specific, approximately linear, activatory effect on RT. Recently, PentonVoak et al. (1996) provided new evidence in favor of this hypothesis. To separate the linear from the non-linear effects due to the interference, a linear regression $X = a + bf$ (with X being the chronometric variable to be analyzed and f being the frequencies) was computed on each elementary condition (right CS congruent trials, right CS incongruent trials, etc...) and for RT, MT and CT. We computed residuals (recorded values–computed values) (Fig. 3b,c). All the

residuals of trials without incorrect activity were averaged to obtain one distribution per subject. According to previous results (Burle and Bonnet, 1997), a zero crossing between 20.5 and 21 Hz is expected. In order not to confound the linear effect of the clicks (Penton-Voak et al., 1996) with the interference effect, statistical analysis was done on residuals, and the degrees of freedom were the same as for the regression analysis.

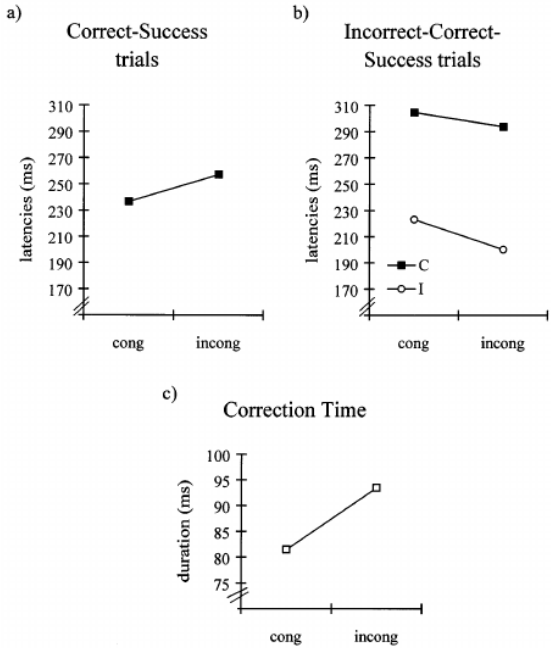

Figure 4: (a) Latency of correct EMG activity as a function of congruency in trials without Incorrect EMG activity (correct– success trials). (b) Latencies of correct (C) and incorrect (I) EMG activities as a function of congruency in trials with an incorrect EMG activity (incorrect-correct-success trials). (c) Correction time as a function of congruency.

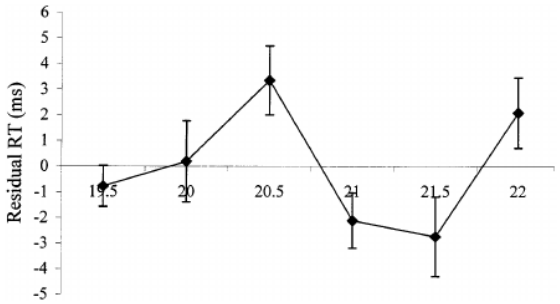

Figure 5: Mean reaction time residues (± S.E.) in eight subjects as a function of click train frequency.

3. Results

The rate of the true incorrect responses (response reaching the force criterion on the wrong side first) was 2.19% for the whole experiment, plus 0.013% for excessively late responses (after 600 ms). The proportion of success trials was, therefore, 97.8%. No factor significantly affected this error rate (t-test computed on the arc-sine of square-root of the error rate (Winer, 1970), d.f.= 7).

3.1. EMG data

Because these data should replicate previous findings (Isnard, 1995), unilateral t-tests were used in statistical analysis. The EMG onset latencies for CS-trials were shorter for congruent situations (237 ms) than for incongruent situations (257 ms) (t7 = 5.55; PB 0.001) (Fig. 4a). The percentage of ICS-trials was higher in incongruent situations (27.5%) than in congruent ones (14.25%) ($t_7 = 3.42; P < 0.005$). In this type of trials, the I-activation onset latencies were earlier in incongruent situations (200 ms) than in congruent ones (223 ms) ($t_7 = 2.57; P < 0.025$). The C-activation latencies were not significantly different in congruent (304 ms) compared to incongruent situations (294 ms) ($t_7 = 1.22; n.s.$). As expected, the CT appeared shorter in congruent situations (81 ms) than in incongruent ones (94 ms) (Fig. 4c). This difference was close to reaching the conventional significance level ($t_7 = 1.79; P = 0.058$). All of these data are replications of previous findings (Isnard, 1995).

3.2. Motor time

Neither congruence (congruent: 40 ms; incongruent: 39.5 ms) nor trial type (CS: 40 ms; ICS: 39.5 ms) affected MT (congruence: $F(1,7) = 1.077; P = 0.33$; trial type: $F(1,7) = 2.38; P = 0.17$ and interaction: $F(1,7) = 0.035; P = 0.86$).

3.3. Effects of clicks

3.3.1. Main effects on RT

Linear effect. The mean linear effect of click train frequencies on the RT was computed for each subject. For all the subjects, the RT decreased as stimulation frequency increased. The mean slope of the decrease (-2.11 ms/Hz) is significantly different from zero ($t_7 = 2.95; P < 0.05$).

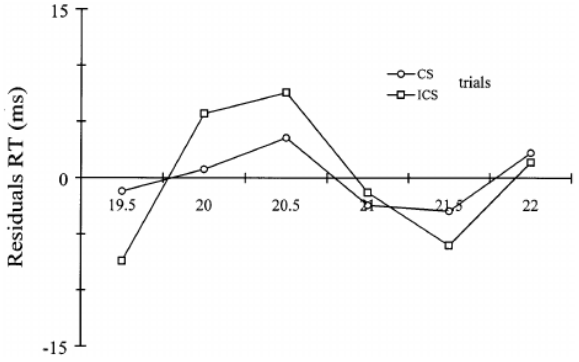

Figure 6: Mean reaction time residues for trials with (ICS) and without (CS) incorrect EMG activities as a function of click train frequency (eight subjects).

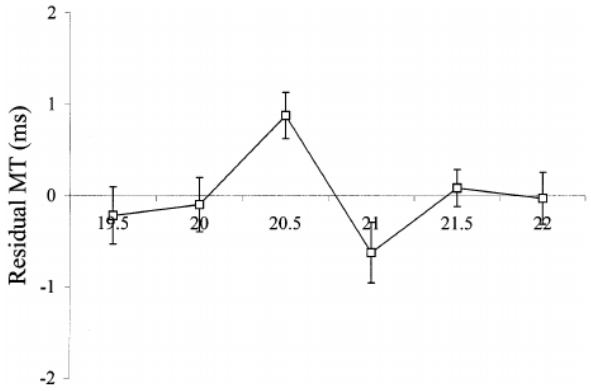

Figure 7: Mean motor time residues (1 ± S.E.) in eight subjects as a function of click train frequency.

Driving effects. After the linear component was removed, a repeated analysis of variance was done on the residual latencies of force deflection onsets (RT) according to the following design: frequency × type of trial (with or without incorrect activity) × congruency. There was a main significant effect of frequency ($F(4,28) = 5.43; P < 0.01$) (Fig. 5). Fig. 6 shows the effect of frequencies as a function of trial types. We noted an increase in the amplitude of the patterns for ICS trials relative to CS trials. This interaction was nevertheless non-significant ($F(4,28) = 1.48; P = 0.23$), but the second order interaction between frequency, congruency and trial type was significant ($F(4,28) = 2.88; P < 0.05$). A more precise analysis showed that the interaction between frequency and trial type did exist for the congruent situation ($F(4,28) = 2.74; P < 0.05$), but not for the incongruent situation ($F(4,28) = 0.53; P = 0.71$). The interaction between frequency and congruency was not significant ($F(4,28) = 2,14; P = 0.10$). This interaction was close to reaching the conventional significance level for ICS trials ($F(4,28) = 2,62; P = 0.056$), but disappeared for CS trials ($F(4,28) = 1,24; P = 0.32$).

3.3.2. Effects on motor time

Because neither congruence nor trial type affected it, MT values obtained in these various conditions were averaged for each frequency. To suppress any possible activatory effect of the external periodic stimulation, a linear regression was computed on the 6 means (one per frequency). Interference patterns were sought in the residual distribution. The predicted interference pattern (between 20.5 and 21 Hz) was found (Fig. 7). MT variations, although very small (1.5 ms), were close to reaching the conventional significance level (F(4,28)=2.53; P = 0.06).

3.3.3. Correction time

No effect of the clicks was obtained on the CT, either as a main effect (F(4,28) = 0.45; P = 0.77) or as an interaction with congruence (F(4,28) = 0.54; P= 0.71).

4. Discussion

4.1. Is there an effect of auditory foreperiod duration?

The drastic onset of the click train could serve as a supplementary preparatory signal. As the RS was always synchronized with a click (see method), the time of this onset according to the RS was not constant across the frequencies (Table 1). As the small variations of the foreperiod ranging from 488 to 524 ms look like the modulations of the RT, as a mirror image, a possible role of these variations must be addressed. Indeed, the RT is known to be dependent on the duration of the foreperiod (FP), that is the time elapsing between a warning signal and the RS (Bertelson and Tisseyre, 1969). For exemple, the RT is shorter when the FP is 500 ms than when it is 2500 ms (Hasbroucq et al., 1997), because the temporal uncertainty on the date of occurrence of the RS is lower for 500 ms than for 2500 ms (Requin et al., 1991). Could it be that the small variations of the auditory FP is responsible for the RT variations we obtain? Let's suppose that the temporal preparation is lower for the 488 ms FP (20.5 Hz) than for the 524 ms (21 Hz), thus leading to an increase (20.5 Hz) followed by a decrease (21 Hz) in RT. In this case, the RT is negatively correlated with the FP duration, thus leading to an artefactual interference pattern. This possible artefact was already evaluated in Burle and Bonnet (1997). The conclusion was that the effect of the foreperiod variation, if it exists, could not explain the RT modulations. Now if we compare the two experiments, a further argument against this artfact is provided. In Burle and Bonnet's (1997) experiment, the RT variations were the same as in the present experiment, whereas the variations of the FP were opposite (Table 1): Increases in RT due to adjoining frequencies (20.5 and 20.6 Hz) fitted in one experiment to a short FP (488 ms, present study), and in another experiment to a long FP (534 ms, Burle and Bonnet, 1997). As a variation of an experimental factor cannot led to both an effect and its opposite, it seems unlikely that the RT variations could be explained by a difference in temporal preparation due to the FP variations.

4.2. Functional role of the internal clock

One of the major goals in the present experiment was the clear replication of the results of Treisman et al. (1992) and

Burle and Bonnet (1997). Indeed, according to these studies, an interference effect was expected between 20.5 and 21 Hz, and that is exactly what we did obtain. Thus, both Treisman's protocol, and the hypothesis of an internal clock which paces information processing, are strengthened. The fact that the amplitude of the interference pattern is increased in trials presenting an incorrect activity (ICS), where the number of betweenstage transmissions is increased, suggests that the internal clock paces transmissions from one stage to the next. Nevertheless, this increase was only significant for congruent trials. This difference between congruent and incongruent trials was unexpected. It could be due to a non-homogeneous population of ICS trials in the incongruent situation. There is more ICS trials in the incongruent situation than in the congruent one. In the congruent situation, the I-activation should be mainly due to a strategic preparation, before the RS, of the alternative response. This kind of I-activation is obviously present in the incongruent situation. In addition, in this situation, another population of I-activation should be due to an automatic incorrect response activation by the position of the signal (contralateral to the response side) (Eriksen et al., 1985). In this case, the ICS population in incongruent trials is a compound of two kinds of trials. This could make the RT distributions more noisy, and thus could hide the interaction effect. Nevertheless, this two-population hypothesis has not been clearly demonstrated, and this ad hoc interpretation should be taken with caution. The information pacing hypothesis is close to Dehaene's proposals (1993). To explain the periodicity he observed in RT distribution, Dehaene (1993) suggested that the visual system picks up information at discrete moments or perceptual episodes (Stroud, 1955; Andrews et al., 1996) and, thus, induces packets of information (Dehaene, 1993; Bringuier et al., 1997). The information processing system has to deal with those packets. For each of them a decision is made: either to transmit the results of the processing to the next stage, or to wait for and integrate the following packet. In the latter case, more complete information would be transmitted to the next stage. This mechanism would take place at each stage of information processing. If this segmentation is due to the internal clock, then its slowing down (or its speeding up), due to external stimulation, would lead to an increase (or a decrease) of processing time within each stage, as well as an increase (or a decrease) of the period between two possible moments for transmission. Furthermore, an extension of these concepts to the motor side can explain the modulations of the MT. Recent findings on oscillations in motor areas suggest that the cortical motor command is periodically sent through the cortico-spinal tract with a frequency at about 20 Hz (Conway et al., 1995; Baker et al., 1997; McAuley et al., 1997). The periodic stimulation we used could interfere with the internal clock responsible for the periodic command, and then increase (or decrease) the time between two packets of the descending information in the cortico-spinal track. As a result the mean frequency of discharges in the cortico-spinal track, which determines the rate of motor units recruitment in hand muscles (Kukulka and Clammann, 1981; Seki and Narusawa, 1996), would be decreased. This rate is known to be negatively correlated with the MT (Hasbroucq et al., 1995). Thus, a decrease (increase) in the cortico-spinal frequency discharge, due to the external stimulation, would lead to an increase (decrease) in the MT.

4.3. A tentative model of the role of the internal clok in information processing and its possible relation to cortical oscillations

According to the proposals made above and to recent data in the literature, we can propose the following mechanism. Recent data have pointed out the existence of oscillations in the motor cortex (Pfurtscheller et al., 1993; Nashmi et al., 1994; Murthy and Fetz, 1996a,b; Roelfsema et al., 1997) whose frequency are very close to the internal clock one (Treisman et al. 1992; Burle and Bonnet, 1997; present study). These oscillations seem to be related to an aspecific motor preparation (Nashmi et al., 1994). In addition, the cortico-spinal excitability has been shown to decrease during the FP in a RT task, (Bonnet et al., 1981; Hasbroucq et al., 1997) and this result has been interpreted as a mechanism to increase signal/noise ratio (Hasbroucq et al., 1997). These two phenomena are probably due to the same mechanism, for several reasons. Firstly, they appear at the same time over the same structures, that is, over the motor cortex when the subjects prepare themselves to react. Secondly, the interneurons responsible for the oscillations are inhibitory (Llinás et al., 1991; Whittington et al., 1995), and are acting as a clock on pyramidal cells (Jefferys et al., 1996). Their firing can be at the origin of the cortico-spinal inhibition described by Hasbroucq et al. (1997). Finally, according to Lisman's (1997) proposals, one way to increase the signal/noise ratio is to code information by bursts of spikes, and one way to generate bursts is to make the neurons oscillate. Therefore, during the FP of a RT task, the temporal preparation (Requin et al., 1991) could be achieved by putting the involved structures in an oscillatory state (Roelfsema et al., 1997), and, hence, preparing them to receive packets of information (Dehaene, 1993) coded in bursts (Bringuier et al., 1997). The neurons in these structures would then be strongly receptive to such a message, but less receptive to external stimulation (electrical or magnetical) used to access the excitability of the motor structures. In conclusion, we propose that when working under temporal constraints which require attentional control (RT task), the central nervous system processes and transmits information by packets. These packets would be coded by bursts of spikes periodically distributed in time (Bringuier et al., 1997). The periodic transmission could be gated by a periodic inhibition3 (Jefferys et al., 1996; Bringuier et al., 1997) sent by the internal clock (Treisman et al., 1992; Burle and Bonnet, 1997, present study) which should furthermore pace the excitability of the neurons receiving the information. Thus, the neurons oscillate between non-receptive (inhibited) and receptive states. Since the temporal structure of the packets of information is synchronized to the fluctuation of the input neuron receptivity, the packets always arrive in an excitable phase of the neuronal oscillation. This leads to a very reliable transmission. In contrast, all spikes which are not in phase with receptive states will not produce a sufficient post-synaptic excitation to counteract the periodic inhibition. This double pacing of both incoming information

and receptive states should greatly increase the signal/noise ratio. Up to now we cannot decide whether the frequency of this inhibition is around 40 or around 20 Hz, for two reasons : these values are harmonics, and, second, both 40 Hz (Pfurtscheller et al., 1993) and 20 Hz (Conway et al., 1995; Roelfsema et al., 1997) oscillations have been reported over the motor cortex. The cortical oscillations could then serve as an internal clock (Treisman et al., 1994), whose role would be to periodically modulate the excitability of task-related structures, and then to give a temporal format to transmitted messages. Such a process could enable the dissociation between the current information and the cortical noise.

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